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First record of *Mollisquama* sp. (Chondrichthyes: Squaliformes: Dalatiidae) from the Gulf of Mexico, with a morphological comparison to the holotype description of *Mollisquama parini* Dolganov

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Abstract

The description of the pocket shark genus *Mollisquama* (*M. parini* Dolganov, 1984) is based on a single known specimen collected from the Nazca Ridge of the southeast Pacific Ocean. A second *Mollisquama* specimen has been captured in the central Gulf of Mexico establishing a considerable range extension and a parturition locality because the specimen has a healed vitelline scar. Both the holotype of *M. parini* and the Gulf of Mexico specimen possess the remarkable pocket gland with its large slit-like external opening located just above the pectoral fin. Features found on the Gulf of Mexico specimen that were not noted in the description of *M. parini* include a series of ventral abdominal photophore agglomerations and a modified dermal denticle surrounded by a radiating arrangement of denticles just posterior to the mouth. Based on a morphometric and meristic comparison of the Gulf of Mexico specimen with information in the description of *M. parini*, the Gulf of Mexico specimen is identified as *Mollisquama* sp. due to differences in tooth morphology and vertebral counts. Phylogenetic analysis of NADH2 gene sequences places *Mollisquama* sister to *Dalatias* plus *Isistius* within the family Dalatiidae.

Key words: pocket gland, photophore agglomerations, molecular systematics, NADH2, dentition

Introduction

Kitefin sharks of the family Dalatiidae (Squaliformes) comprise 7 genera (*Dalatias*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*, *Isistius*, *Mollisquama*, and *Squaliolus*) of which five are monotypic–the highest percentage of monotypic genera for any family in the order Squaliformes (Ebert *et al.* 2013). Dalatiids are distinguished from other squaliform sharks by their snout shapes, strong jaws, lower teeth with high-bladelike crowns, dorsal fins without spines (except *Squaliolus*), and the lack of an anal fin. They are distributed world-wide in most temperate, subtropical and tropical marine waters and their life histories, distribution ranges and behavior are often based on few museum specimens and a paucity of reliable observations. Dalatiids are viviparous (Gadig & Gomes 2002) with embryos nourished in utero by a yolk sac. Some species are known to be luminescent (Claes *et al.* 2014), a feature that may aid in attracting prey or as counter-illumination to facilitate predatory behavior. Sharks of the genus *Isistius* (cookie cutter sharks) employ a unique feeding behavior that allows them to use their cookie-cutter-like teeth to excise a nearly symmetrical oval flesh plug from a variety of prey species including marine mammals, tunas, billfishes, and squids (Strasburg 1963, Shirai & Nakaya 1992). Dalatiids in general possess relatively similar dentitions and jaw structures.

One of the rarest monotypic dalatiids, *Mollisquama parini* Dolganov, 1984 was described from a single female specimen collected from the Nazca Submarine Ridge in the southeast Pacific Ocean (Dolganov 1984; translation provided by N. Donoho, pers. comm.). *Mollisquama parini* is unique within Squaliformes because of distinctive dermal denticle morphology and conspicuous external slits that form the opening to a villi-lined internal pocket

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gland located just above each of the pectoral fin bases; no other species of dogfish shark possess those features (Compagno *et al.* 2005, Ebert *et al.* 2013). A second *Mollisquama* specimen was captured during a 2010 midwater trawl survey of the northern Gulf of Mexico (GoM) conducted by NOAA/NMFS Southeast Fisheries Science Center, Mississippi Laboratories (MSL). The survey was conducted to explore possible fish and invertebrate prey associated with sperm whale aggregations. The *Mollisquama* specimen was identified by the marine mammals research group as a dalatiid shark and was retained as part of a specimen collection that was archived at MSL. Herein is the description of the external morphology and dentition of the GoM *Mollisquama* specimen with comparisons to the description of the holotype of *M. parini* Dolganov (1984) (not examined by the authors). Taxonomic implications resulting from a molecular phylogenetic analysis of mitochondrial DNA sequence data from the GoM specimen and other dalatiid sharks are also discussed. To date no other specimens of *Mollisquama* have been reported.

Material and methods

After a preliminary inspection and photography, the specimen was archived frozen in water until it was later examined in the laboratory (October 2013). A portion of the right side pectoral fin was removed for DNA analysis before the specimen was preserved in 20% formalin. After 21 days the specimen was rinsed and soaked in freshwater for 24 hours to remove formalin, then transferred to a solution of 35% ethanol for two days, and is now permanently stored in 70% ethanol. The pectoral fin tissue sample was preserved in undiluted 95% ethanol and stored at -80°C. Both the specimen and the pectoral fin tissue are accessioned under catalog number TU 203676 in the Royal D. Suttkus Fish Collection archived at the Tulane University Biodiversity Research Institute, Belle Chasse, LA.

Measurements were made from the left side of the specimen and follow Compagno (1984) unless otherwise noted (ceratotrichia that extend as filaments past fin margins were not included in measurements); measurements and feature descriptions were made from the preserved specimen. Tooth descriptions follow Seigel (1978) and are for medial teeth unless specifically designated. All visible teeth were counted in each jaw; however, tooth counts should be considered preliminary since the jaws were not removed and smaller lateral teeth could have gone unnoticed. Several lower jaw medial teeth were missing thus preventing an accurate tooth count (2.9 mm gap between the remaining 12 lateral teeth of each side of lower jaw). To estimate lower tooth count, crown base measurements were made for the teeth immediately flanking each side of the gap (mean crown base width 0.4 mm). Considering medial teeth for most sharks are relatively larger than successive lateral teeth (Ebert *et al.* 2013), an estimated seven lower teeth would adequately fill the gap (estimate includes a center symphyseal tooth as documented for the holotype). Vertebral counts were made from a radiograph and the counts followed the holotype groupings of trunk (first vertebra to pelvic fin insertion), caudal peduncle (pelvic fin insertion to caudal fin upper lobe origin), and caudal (caudal fin upper lobe origin to the last discernable vertebra); dissecting pins separated vertebrae groupings. Vertebral counts were made with the aid of a binocular dissecting scope.

A portion of the right-side pectoral fin was provided to the Hollings Marine Laboratory (Charleston, SC) and total DNA was extracted using High Pure PCR Template Preparation Kit by Roche Diagnostics[1] (Indianapolis, IN). Extracted total DNA was stored at -20° C until used for PCR amplification. Samples were amplified using Fermentas Taq with ASN and ILE primers (Naylor *et al.* 2005) designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (NADH2). The PCR product was sent to Retrogen (San Diego, CA) for ExoSAP-IT purification and sequencing. Sequences were translated to amino acids and aligned along with representatives from closely related taxa following Naylor *et al.* (2012) using the software package MUSCLE (Edgar 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences to yield a nucleotide alignment. A maximum likelihood analysis of the aligned nucleotide sequences was conducted under the GTR +I + G model of molecular evolution.

Two small pieces of skin (approximately 2.0 mm x 5.0 mm) were removed from the right side dorsolateral area below the first dorsal fin to examine using scanning electron microscopy (SEM). The skin was dehydrated in a

1. The mention of any product names or Web-based links does not constitute endorsement by the Department of Commerce/ National Oceanic and Atmospheric Administration/National Marine Fisheries Service/Mississippi Laboratories.

series of ethanol solutions (70%, 80%, and 90%) for ten minutes each then was stored in 100% ethanol. Skin samples were prepared for SEM by critical point drying using a Tousimis Autosamdri 814 apparatus and then were coated with gold dust. The dermal denticle crowns and surface of the skin were examined with a Hitachi S-4800 field emission SEM under 30–90,000 times magnification.

Specimen condition. The specimen was dead when initially sorted from the catch (catch sorting is generally completed within 30 min. after the net haul). A vertical dermal lesion of unknown origin (approximately 10.0 mm in length and located between the right eye orbit and snout) was present when the specimen was first examined prior to freezing (Fig. 1A). The vertical lesion may have resulted either from contact with other specimens or with the trawl, or from significant body swelling (relative to the preserved specimen) that is apparent in photographs taken when the specimen was first landed. Body swelling was to the extent that the base of the vertical lesion is pulled open almost equal to the eye's horizontal diameter (hemorrhaging is visible within the lesion), eye orbits were horizontally and vertically stretched and spiracles were vertically stretched about double their horizontal length (the GoM's spiracles measured after freezing and preservation are horizontally longer than their vertical height). Also noted from photographs taken when the specimen was first landed is that the upper lip appears to be considerably swollen and there was capillary hemorrhaging along all lips and on the roof of the mouth (Fig. 1B). Other features that were affected by the swelling include gill slits that were vertically stretched to the point that the gill openings were closed, and the pocket's outer margin was slightly protruded (probably due to the underlying swollen tissue). After the specimen was preserved the body ground color was slightly faded and there was dermal peeling of the rear portion of the second dorsal fin and around the opening of the left-side spiracle, and three shallow folds formed along the right-side trunk; the hemorrhaging along lips became dark brown in color. Preserved with the specimen are teeth removed for dentition descriptions and a plug of soft non-descript opaque tissue that was lodged in the rear of the buccal cavity. Most of the right pectoral fin was removed to use as tissue for extracting DNA.

FIGURE 1. *Mollisquama* sp., TU 203676 (142.0 mm TOT), photographs taken before preservation (A) right lateral view and (B) ventral view. Scale bar is 10 mm in both figures.

Results

Trawling effort, environmental parameters, and associated catch summary. The specimen was captured at

survey station 053 (26° 18'33"N, 089° 25'45"W) approximately 170 nautical miles (n. mi.) south of the Mississippi River Delta, and 30 n. mi. north of the U.S. Exclusive Economic Zone GoM southern boundary. The maximum bottom depth beneath the trawl path was 3038 m and the maximum depth for the mid-water trawl was 580 m; the trawl is effective beginning just below surface once the trawl doors spread (generally within 5 m of surface). Trawl start time was 07:01 am U.S. central standard time (1201 GMT) on 4 February 2010 and tow duration was two hours. Even though environmental sampling was not conducted specifically at the trawl location, there was environmental sampling (sensor array) for a marine mammal search station within 10 n. mi. of the trawl location immediately prior to the trawl event. At the marine mammal search station sea surface water temperature at 2.0 m depth was 21.5°C, oxygen saturation was 6.6 mg/l, and salinity was 36.5 ppt. For the equivalent maximum trawl depth (580 m) the sea water temperature was 7.2°C, oxygen saturation was 4.0 mg/l, and salinity was 34.9 ppt. Other fauna captured during the mid-water trawl tow included finfish, cephalopods, decapods, and tunicates.

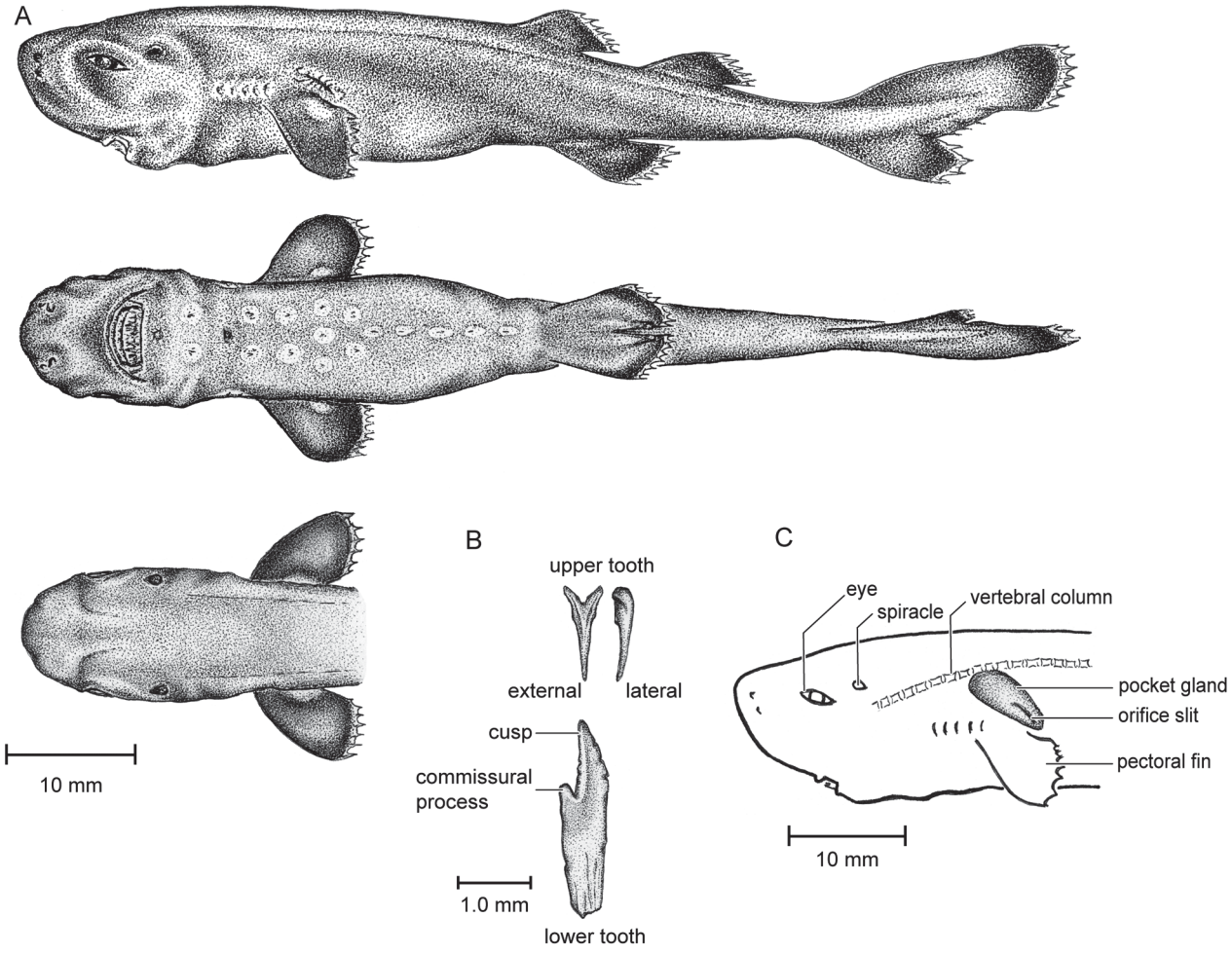

FIGURE 2. *Mollisquama* sp., TU 203676 illustrated to scale. (A) Lateral, ventral and partial dorsal view of head and posterior to the pectoral fins. (B) Upper (external and lateral view) and lower (external view) of tooth number 4 from the right side of *Mollisquama* sp.. (C) Diagram of the location and size of the pocket gland and external orifice of *Mollisquama* sp. interpreted from a radiograph.

General description. Male *Mollisquama* sp. (Fig. 2) weight 14.6 g and total length (TOT) 142.0 mm; other measurements and percentage of TOT or head length (HDL) Table 1. Body cylindrical anteriorly and somewhat laterally compressed for posterior two-thirds; tapers towards a slender caudal peduncle nearly circular in cross section at caudal fin origin. No caudal keels or precaudal pits. Head large and wide and considerably deeper than rest of body; greatest width just posterior to spiracles. Sensory pores not immediately visible from superficial examination and if present covered by denticles. Bulbous snout short, blunt, and rounded in profile and widest just posterior of nostrils. Subterminal mouth originates beneath posterior half of orbit and jaws approximately equal length. When mouth is closed lower jaw teeth cover those of upper jaw (underbite). When mouth is opened orifice

irregularly rectangular (anterior margin of lower lip nearly horizontal); prominent lateral lips join upper and lower lips and conceal mouth corners. Anterior facing surface and posterior surface of upper lip smooth and lower edge crenate. No upper labial furrows or lower labial folds. Oral furrows begin at outer margins of upper jaw and terminate below spiracles; dermal denticles within oral furrow and surrounding it. Nostrils small and directed forward with incurrent apertures spaced further apart than excurrent apertures. Orbits slope slightly downward in a shallow concavity (about 1.0 mm deep) that begins dorsally 2.0 mm above eye, expands to 5.0 mm width in level with eye (where it reaches its maximum depth), tapers and terminates 4.0 mm below eye; particularly noticeable in frontal views and delineates posterior contour of snout. Orbits elliptical and about three times longer than height. Outer periphery of eye overlapped with an eyelid of 1–2 mm. Eyes positioned level with nostrils and anterior to and just ventral of spiracles. Gill slits small; second is smallest and progressively larger to fifth slit (Table 1). Healed vitelline scar (previous attachment point for a yolk stalk) located medially 13.0 mm posterior of mouth.

TABLE 1. Comparison of morphometric values between the Gulf of Mexico (GoM) *Mollisquama* sp. and the holotype. Measurement abbreviations are from Compagno (1984).

Feature		GoM mm	GoM %TOT (142.0 mm)	GoM % HDL (33.9 mm)	Holotype %TOT (400.0 mm)	Holotype %HDL (73.2 mm)
Measurements between distinguishing features						
Pocket origin to pectoral fin origin		8.30	5.85			
Pocket origin to pectoral fin base		2.50	1.76			
Dorsal fin 1 to dorsal fin 2	IDS	12.37	8.71*		11.80	
Dorsal fin 2 to caudal fin upper lobe	DCS	16.44	11.58*		9.50	
Pectoral fin origin to pelvic fin origin		39.00	27.46*		37.30	
Pelvic fin to caudal fin lower lobe	PCA	27.00	19.01*		14.00	
Gill slit 1–5	ING	6.50	4.58			
Measurements from snout tip to origin of						
Nostril incurrent aperture	PRN	3.80	2.68			
Eye orbit	POB	9.85	6.94	29.05*		27.40
Spiracle	PSP	17.90	12.61			
Upper jaw medial point	POR	15.25	10.74			
Gill slit 1	PGI	27.40	19.30			
Gill slit 5	HDL	33.90	23.87*	100.00	18.30	100.00
Pectoral fin	PP1	33.09	23.30			
Vitelline scar		27.45	19.33			
Pelvic fin	PP2	71.73	50.51*		61.00	
Vent (cloaca)	SVL	80.48	56.68			
Dorsal fin 1	PD1	66.81	47.05		45.80	
Dorsal fin 2	PD2	84.94	59.82			
Upper caudal fin lobe	PRC	108.50	76.41			
Lower caudal fin lobe		108.00	76.06			
Caudal fin fork (fork length)	FOR	123.80	87.18			
Snout tip to abdominal glands (count:inter space mm)						
Row 1 (2:5.84)		23.35	16.44			
Row 2 (2:5.30)		31.06	21.87			
Row 3 (2:5.30)		35.50	25.00			

.....continued on the next page

TABLE 1. (Continued)

Feature		GoM mm	GoM %TOT (142.0 mm)	GoM % HDL (33.9 mm)	Holotype %TOT (400.0 mm)	Holotype %HDL (73.2 mm)
Row 4 (3:4.40)		40.60	28.59			
Row 5 (2:4.10)		44.10	31.10			
Row 6 (1)		46.90	33.03			
Row 7 (1)		52.02	36.63			
Row 8 (1)		57.40	40.42			
Row 9 (1)		61.25	43.13			
Row 10 (1)		65.70	46.27			
Head						
Width	HDW	15.20	10.70		10.80	
Height	HDH	19.40	13.66		14.30	
Nostrils						
Incurrent aperture space		8.81	6.20			
Excurrent aperture space	INW	7.70	5.42			
Nostril width	NOW	2.91	2.05			
Eye						
Length	EYL	5.87	4.13*	17.31	3.26	17.80
Height	EYH	2.10	1.48			
Cornea/pupil diameter		3.50	2.46			
Rear orbit margin to spiracle	ESL	2.49	1.75			
Interorbital width	INO	15.00	10.56*	44.25	8.02	43.83
Mouth						
Width (lower corners)	MOW	9.00	6.34	26.55*		32.90
Length	MOL	0.80	0.56			
Upper jaw furrow		3.78	2.66			
Teeth (left side)						
Upper symphyseal crown height		0.50	0.35			
Upper symphyseal crown base width		0.20	0.14			
Upper 4th crown height		0.83	0.58	2.4		
Upper 4th crown base width		0.20	0.14	0.6		
Lower flanking crown mean height		0.99	0.70	2.9		
Lower flanking crown mean base width		0.39	0.27	1.1		
Spiracle						
Height		2.00	1.41			
Length	SPL	3.00	2.11	8.84		8.90
Gill slits						
1st	GS1	0.96	0.07	2.83		
2nd		0.89	0.63	2.63		
3rd		1.53	1.08	4.51		
4th		1.66	1.17	4.90		
5th	GS5	2.13	1.50	6.28*		10.30

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TABLE 1. (Continued)

Feature		GoM mm	GoM %TOT (142.0 mm)	GoM % HDL (33.9 mm)	Holotype %TOT (400.0 mm)	Holotype %HDL (73.2 mm)
Pocket						
Length		4.22	2.97	12.45*	3.00	16.39
Width		2.00	1.40	0.59		
Pectoral fin						
Base	P1B	8.25	5.81			
Anterior margin	P1A	14.04	9.90*	41.42*	11.50	63.00
Posterior margin	P1P	8.20	5.77			
Length	P1L	12.75	8.98			
Height	P1H	10.40	7.32			
Inner margin	P1I	4.50	3.17			
Dorsal fin 1						
Base	D1B	7.70	5.42*		6.00	
Anterior margin	D1A	7.45	5.25			
Posterior margin	D1P	5.70	4.01			
Length	D1L	13.27	9.35			
Height	D1H	4.78	3.37		3.40	
Inner margin	D1I	5.57	3.92			
Dorsal fin 2						
Base	D2B	8.95	6.30*		7.50	
Anterior margin	D2A	7.00	4.93			
Posterior margin	D2P	7.02	4.94			
Length	D2L	12.45	8.77			
Height	D2H	3.65	2.57*		3.00	
Inner margin	D2I	3.50	2.46			
Pelvic fin						
Base	P2B	7.73	5.44*		9.30	
Anterior margin	P2A	12.30	8.66			
Posterior margin	P2P	6.75	4.75			
Length	P2L	16.8	11.83			
Height	P2H	5.53	3.89		4.00	
Inner margin	P2I	7.80	5.49			
Clasper inner margin	CLI	5.38	3.79			
Clasper outer margin	CLO	0.31	0.22			
Caudal fin						
Caudal peduncle height	CPH	4.62	3.25			
Upper lobe	CDM	33.00	23.24*		19.50	
Lower lobe	CPV	19.82	13.96*		11.50	
Upper postventral caudal margin	CPU	11.34	8.00			
Lower postventral caudal margin	CPL	5.79	4.08			
Caudal fork width	CFW	9.54	6.72			
Caudal fork length	CFL	18.20	12.82			
Terminal caudal lobe	CTL	6.86	4.83			

*Exceeds +/- 5% of holotype %TOT or holotype %HDL.

Two low-profile spineless dorsal fins. First dorsal fin origin slightly anterior to body midpoint; insertion above pelvic fin origin. Interdorsal length less than caudal peduncle length. Length of second dorsal fin base greater than first. Pectoral fins small with broadly rounded apex and origin just anterior of last gill slit. Pelvic fins small and triangular and paired claspers not firm and do not extend past pelvic fin inner margins. Anal fin absent. Caudal fin lower lobe 60% length of caudal fin upper lobe; both lobes relatively broad with rounded apex. Ceratotrichia that extend as filaments past rear margins of all fins less than 2.0 mm long.

Thirty-seven monospondylous vertebrae (trunk) and 31 diplospondylous vertebrae (17 caudal peduncle, 14 caudal). Radiograph resolution of terminal caudal vertebrae not optimal and affected by low vertebral calcification (typical for young chrondrichthyans); counts interpreted as preliminary because of low resolution.

Coloration. Dorsal surface of head and body light gray with brownish undertones. Lateral line pigmented slightly darker than background body color from above gill slits to caudal peduncle. Ventral surface darker gray to black. Lighter pigmentation around and within mouth and area between gill slits cream colored distinct bar. Fins slightly darker than body. Pectoral fins nearly uniform dark grey except for pale blotch at posterior half of both dorsal and ventral sides of base. Pelvic fins darker towards posterior margins. Both dorsal fins darker than body ground color and distal portions of caudal fins black. Rear edges of fin margins lightly pigmented where fin ceratotrichia extend as filaments past rear margins. Numerous dark specks generally arranged around dermal denticle pedicle bases and many times smaller than dermal denticles.

Teeth. Lower jaw tooth count estimate 15–1–15 and upper jaw tooth count 9–1–9. Teeth exhibit dignathic heterodonty; crowns for upper teeth much more slender and shorter than broader and longer crowns of lower teeth (Fig 2B). Both upper and lower teeth decrease in size toward mouth corners. In proportion to HDL, upper tooth crown height 2.4% and crown base width 0.6%; relatively larger lower tooth crown height 2.9% and crown base width 1.1%. For outer tooth rows upper and lower teeth crown bases exposed below gum line margin.

Lower teeth have high-triangular crowns and when progressing from center cusps increasingly curve toward mouth corners. Lower teeth with distinct commissural process along lateral margin of crown base that overlaps lateral margin of crown base of adjacent tooth. No distinct crown or cusp serrations for lower or upper teeth but irregularly spaced shallow notches along lower teeth crown margins. Lower jaw teeth root striated. Outer row of lower teeth not firmly anchored and when gently probed move as a group of 4–5 teeth.

Upper teeth narrow with broad forked root, and generally stacked in three visible rows with distal tip of outer teeth recessed above lower replacement teeth. Upper teeth crowns conical, smooth, and slightly curved posteriorly (Fig. 2B). Upper teeth more firmly anchored than lower teeth.

Pocket gland. Pocket gland discernible as faint outline above pectoral fin in radiograph. Positioned at 45° to longitudinal axis of body (Fig. 2C) and 13.0 mm long and 5.0 mm maximum width (dorsally between vertebrae 8–12). Pocket gland tapers from its maximum width towards external pocket orifice. External orifice 4.2 mm long and originates 2.5 mm above pectoral fin base (Fig. 2A, C) and slopes approximately 45° posteriorly to just below fin base. Tissue at corners of external orifice lighter bluish-grey. Margin of external orifice crenulated with 14 shallow dermal folds slightly raised above surrounding tissue. Internal tissue past crenulations light grey progressing to much darker inner cavity lined with numerous dark villi. Width of external orifice including dermal folds about 2.0 mm.

Ventral abdominal photophore agglomerations. Series of putative photophore agglomerations (at least 16) along abdominal ventral surface arranged in ten rows consisting of one to three agglomerations in each row (Figs. 1B, 2A). First row consists of a pair 8.1 mm posterior to lower jaw medial point, and last row a single 14.8 mm anterior to vent (cloaca). Agglomerations approximately uniform in size and no noted secretions before or after preservation. Agglomerations not raised above surrounding body and capping denticles uniformly cover in same rostro-caudal orientation as generally found for denticles on rest of body. Lighter bluish-gray area (2.0–4.0 mm diameter) with diffuse outer margin (Figs. 1B, 2A) surrounding darker agglomeration center; diffuse outer margin irregularly rounded for rows 1–5 and more oval shaped for rows 6–10. No distinct center pore visible beneath capping denticles but numerous small dark specks clustered around and between denticle pedicle bases; no discernable features for dark specks and they lack distinct outer ring. Agglomeration capping denticles appear lighter in color than surrounding denticles due to lighter underlying tissue.

Dermal denticles. Lateral trunk dermal denticles loosely aligned in diagonal series and some overlap between denticles (Fig. 3A) with rows of larger denticles irregularly interspersed by rows of smaller. Overlapping of adjacent denticle crowns more prevalent at fin bases and dermal denticles cover all fins but not along posterior

margins of fins. Crowns spatulate, with wider dimension anteriad and tapering slightly posteriorly. Medial projection with concave depression on anterior end of each crown. Mean denticle dimensions 0.7 mm length and 0.4 mm width (measured from Figure 3A, n = 12). Crown surfaces covered with numerous concavities (termed ectodermal pits by Hertwig 1874; cited in Raschi & Tabit 1992) in four longitudinal rows each with five or six pits (mean = 5.4); two medial rows wider than lateral rows. Ectodermal pits decrease in size towards posterior end of denticle. Ectodermal pit edges sharply ridged and form raised peaks at pit confluences that extend length of ridges. Denticles slightly arched and ridges prominent when viewed laterally. Narrow denticle pedicle pigmented darker than crown (at pedicle center), which contributes to speckling along most of body. Pedicle basal plate star-shaped with four points; lateral outer and anterior tips extend beyond crown margin (Fig. 3B).

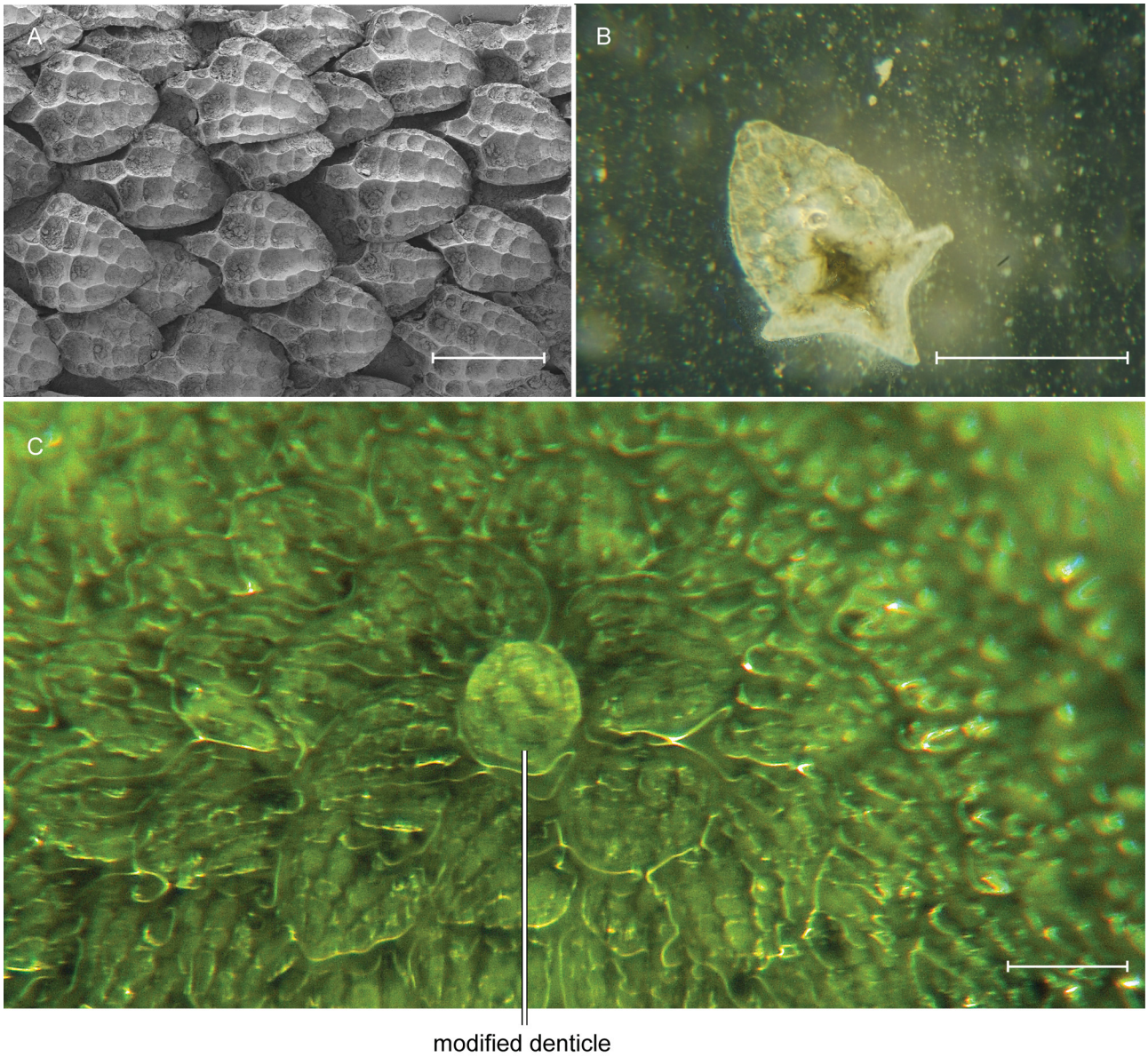

FIGURE 3. Dermal denticles of *Mollisquama* sp., TU 203676. (A) SEM micrograph of denticles from the upper right flank beneath the first dorsal fin; anterior is to left. (B) Single dermal denticle removed from the ventral surface illustrating its translucent property. (C) Modified dermal denticle located 2.5 mm posterior of the mouth; anterior is up. Scale bar is 0.5 mm in all figures.

Uniform dermal denticle morphology for all body areas. Dermal denticles somewhat translucent (Fig. 3B); particularly evident for body areas not darkly pigmented (e.g. gill slit area, pectoral fin bases, ventral abdominal photophore agglomerations, and pocket orifice corners). Dermal denticles in proximity to mouth smaller than those from other body areas. Denticle pedicles surrounded by dark specks presumed to be photophores.

At 2.5 mm posterior of lower jaw (Fig. 2A) radiating arrangement of outward-pointing dermal denticles surround central modified denticle (0.5 mm diameter). Modified denticle with irregularly rounded crown ringed with low nodules and with two half-circle wedges at center separated by groove (Fig. 3C). Modified denticle raised above skin approximately equal in height to surrounding denticles. Narrow surrounding zone of exposed skin (without denticles) between modified dermal denticle pedicle and radiating denticles.

DNA sequencing and phylogenetic analysis. Sequence data for NADH2 gene determined for five of seven genera currently included in family Dalatiidae (*Dalatias, Euprotomicrus*, *Isistius, Mollisquama,* and *Squaliolus*); tissue samples of *Euprotomicroides* and *Heteroscymnoides* not available for sequencing. Full protein-coding alignment 1044 nucleotides long. Mean pairwise sequence divergence among dalatiid species 16.7% and range 8.43%–21.3% for pairs of *Squaliolus aliae*/*Euprotomicrus bispinatus* and *Mollisquama* sp./*E. bispinatus*, respectively. Sequence from S*qualus acanthias* used as outgroup for phylogenetic analysis. Maximum likelihood tree places *Mollisquama* in Dalatiidae and sister to clade containing *Dalatias* and *Isistius* (Fig. 4). *Squaliolus* and *Euprotomicrus* form basal clade of family (http://sharksrays.org/; accessed 31 March 2015).

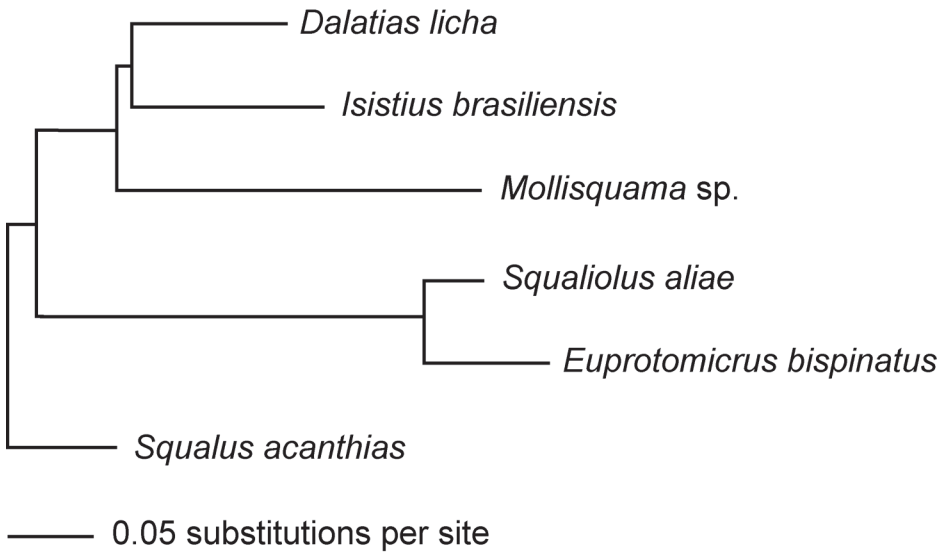

FIGURE 4. Maximum likelihood phylogenetic tree based of sequences of NADH2 for species of family Dalatiidae. *Squalus acanthias* (Squalidae) was used for an outgroup.

Discussion

The enigmatic genus *Mollisquama* has received scant attention from researchers since the southeast Pacific Ocean holotype was described in 1984, but with the capture of a second specimen collected from the Gulf of Mexico additional features not documented for the holotype can now be described. Histology is needed to better understand the composition and function of several important distinguishing features found on the Gulf of Mexico specimen (e.g. ventral abdominal photophore agglomerations and the modified dermal denticle posterior of the lower jaw), and for some of those features a holotype inspection is needed to confirm presence or absence (requests for inspection of the holotype or confirmation of holotype features are pending at the Zoological Institute, St. Petersburg, Russia). Without examination of the holotype the comparisons are based solely on its description (Dolganov 1984) and photographs provided by the Zoological Institute. The result of the phylogenetic analysis is of particular importance because it is the first to include *Mollisquama* and confirm its placement in Dalatiidae.

Specimen condition. Even though the causes of the body swelling that was documented by photographs taken soon after capture cannot be specifically attributed, potential factors that can be defined by data elements include sea water and ambient air temperatures, dissolved oxygen, salinity, and pressure changes related to trawling depths. From sea surface to maximum trawl depth the sea water temperatures ranged from 21.5–7.2°C (ambient air temperature was 22.0°C), dissolved oxygen values ranged from 6.6 – 4.0 mg/l, salinity ranged from 36.5 – 34.9 ppt, and the maximum trawl depth was 580 m. Swelling was considerably reduced after freezing the specimen in water.

Pocket and ventral abdominal photophore agglomerations. The extraordinary pocket gland of *Mollisquama* is unique among cartilaginous fishes and may only be comparable to the luminous abdominal pouch of the dalatiid shark *Euprotomicroides zantedeschia* Hulley & Penrith (1966). The description of *E. zantedeschia* was based solely on the holotype and the authors did not make mention of the abdominal pouch (Hulley & Penrith 1966). Stehmann & Krefft (1988) redescribed *E. zantedeschia* including details on the anatomy of the abdominal pouch and commented on its function after observing a live specimen. Remarkably, the second specimen of *E. zantedeschia* was observed alive immediately after its capture and before preservation. The specimen emitted a bright blue shine from the cloacal area and it secreted a light-blue colored fluid when it was placed into formalin for fixation (Stehmann & Krefft 1988); the blue-colored fluid is also visible in a photograph taken from a third specimen captured during 2008 (http://forum.przyroda.org/topics58/chile-vt10043,30.htm accessed 31 March 2015). Stehmann & Krefft (1988) proposed that the function of the abdominal pouch was to secrete a luminous fluid to attract potential prey or mates, or to elude predators. There is histologic evidence that the tissue of the pouch may be luminescent as well (Munk & Jørgensen 1988).

The orifice of the pocket gland of *Mollisquama* is relatively large (4.2 mm, 2.97% TOT in the Gulf of Mexico specimen and 12.0 mm, 3.00% TOT in *M. parini*) and has physical characteristics that are similar to *E. zantedeschia*. In particular, the raised dermal folds around the margin of the opening, the presence of numerous internal villi, and color. Dolganov (1984) described the gross morphology of the pocket glands in *M. parini* and surmised that they might function to produce and secrete pheromones to attract potential mates.

The description of *M. parini* (Dolganov 1984) did not mention ventral abdominal photophore agglomerations even though they are readily obvious on the GoM specimen. It was not possible to discern the presence of the agglomerations from a photograph of the holotype of *M. parini* because of the orientation of the specimen and due to sutures along the abdomen; therefore, the presence on the holotype should not be ruled out. The abdominal photophore agglomerations span a linear distance of 39.2% of the venter length (snout tip to caudal fin lower lobe origin) and if their function is related to luminosity it is likely enhanced by the relatively translucent dermal denticles (Fig. 3B). With regard to the minute dark specks that are clustered at the agglomeration center, Hubbs *et al.* (1967) described photophores with a single photogenic cell for *Euprotomicrus bispinatus* (Quoy & Gaimard) that are similar to the dark specks found on most of the body of the Gulf of Mexico *Mollisquama*.

Dermal denticles and modified dermal denticle. The dermal denticles of *Mollisquama* are similar to the type I scales described by Reif (1985); the similarity is in their distribution pattern and morphology, in particular, the ectodermal pits. *Dalatias licha* (Bonnaterre), *Euprotomicrus bispinatus*, and *Isistius brasilensis* (Quoy & Gaimard) are other dalatiids that have the unique type I scale morphology, which is adaptive for bioluminescent countershading in mesopelagic habitats (Reif 1985).

Another feature of the Gulf of Mexico specimen that was not noted for the holotype is a modified raised and circular dermal denticle located posterior of the lower jaw (Fig. 3C). Even though the feature cannot be specifically identified from superficial examination, some of the pit organ components in rays can be set on small protuberances (Peach & Marshall 2009; Klimley 2013). If the modified denticle supports pit organ components, the surrounding dermal denticles are not arranged in a pattern typically associated with external pit organs. Peach (2003) and Peach & Marshall (2009) described external pit organ denticle patterns on a rostral-caudal axis as opposed to the radiating arrangement found on the Gulf of Mexico *Mollisquama*; a histological examination is required for assessing the modified denticle's properties (J. Marshall, pers. comm.).

Teeth. There are several differences in the teeth of *M. parini* and the Gulf of Mexico specimen. The Gulf of Mexico specimen has lower jaw teeth that have outer crown margins with irregular shallow notches (Fig. 2B), whereas the holotype has smooth crown margins (Dolganov 1984: fig. B). The Gulf of Mexico specimen has lower jaw teeth that have a single prominent commissural process and they lack a symphysial process on the opposing crown margin, whereas *M. parini* has lower jaw teeth with a double commissural process and a symphysial process on the opposing crown margin. Additionally, the root of the lower jaw teeth of the Gulf of Mexico *Mollisquama* has distinct striations that are lacking in *M. parini*. Upper jaw teeth in the Gulf of Mexico specimen have crowns that are conical (Fig. 2B) and lack the outer longitudinal ridge found in *M. parini* (Dolganov 1984: fig. Γ).

Morphometric comparisons. Due to the rarity of *Mollisquama* in collections and the possibility of undocumented ontogenic allometry, there are no morphometric value ranges useful for identifying the species; however, as a general means of comparing the Gulf of Mexico *Mollisquama* and *M. parini*, morphometric value ranges of +/- 5% of the proportional measurement were applied (Table 1). Holotype proportional measurements

that were at least 5% greater than the corresponding Gulf of Mexico measurement included IDS, pectoral fin origin to pelvic fin origin, PP2, MOW, GS5, P1A, D1B, D2B, D2H, and P2B. Gulf of Mexico *Mollisquama* proportional measurements that were at least 5% greater than the corresponding holotype measurement included DCS, PCA, POB, HDL, EYL, INO, CDM, and CPV. The holotype trunk is proportionally longer than the Gulf of Mexico *Mollisquama* as evidenced by greater PP2 and pectoral fin origin to pelvic fin origin. Conversely, several of the Gulf of Mexico *Mollisquama* anterior and posterior distinguishing features are proportionally longer than the holotype as evidenced by greater HDL, DCS, PCA and CDM.

Several species of Squaliformes exhibit ontogenic allometry that affects proportional differences for distinguishing features of juveniles and large adults (Garrick 1960). One of the most pronounced allometric differences is for an increase in trunk percentage of TOT for large adults; a feature noted in the comparison between the Gulf of Mexico *Mollisquama* and the holotype. Additionally, HDL, CDM, EYL, and a variety of other features have the potential to be proportionally longer in juveniles compared to their adult size classes. For the dalatiid shark (*Dalatias licha*) examined by Garrick (1960), the HDL difference between juveniles and large adults was 8% less for adults. For the Gulf of Mexico *Mollisquama* compared to the considerably larger holotype the HDL difference is 6% less for the holotype.

Vertebrae counts. In addition to morphological differences, the Gulf of Mexico *Mollisquama* total vertebral count was 18% lower than the holotype. For trunk vertebrae the holotype has 42 vs. 37 for the Gulf of Mexico specimen, for caudal peduncle 19 vs. 17, and for caudal 22 vs. 14. Collectively, the corresponding Gulf of Mexico *Mollisquama* vertebrae are proportionally longer than the holotype; 13.5% longer for trunk vertebrae, 11.8% for caudal peduncle, and 57.1% for caudal. For the very small terminal caudal vertebrae, the limitations for detecting calcification with the conventional radiograph may have contributed in part to the low caudal vertebrae count. Springer & Garrick (1964) addressed vertebral count issues for the last few caudal centra by stating that the number of precaudal vertebrae is established early in embryos with the last caudal vertebrae formed in later embryonic life. The Gulf of Mexico *Mollisquama* is past the embryonic stages because it has a healed vitelline scar; therefore, the precaudal vertebral counts are accurate as being fewer in number than the holotype.

Habitat differences. Habitat characterizations for the capture locations of the Gulf of Mexico *Mollisquama* and the holotype are considerably different. The trawling depth (i.e. bottom depth) for the holotype capture was 330 m (Dolganov 1984) from atop the Professor Mesyatzev Seamount, with a nearly flat abyss surrounding sea floor topography at depths ranging from 2000–2500 m (Parin *et al.* 1997) and other seamounts are in proximity (within 30 n. mi.). The maximum trawl depth for the Gulf of Mexico *Mollisquama* capture was 580 m and well off bottom (bottom depth 3038 m) in epipelagic or upper mesopelagic waters; the sea floor topography is abyssal plain with depths over 3000 m and there are no significant bottom features within 120 n. mi. Even though the maximum trawl fishing depths differ between capture locations (330 m vs. 580 m) there is a 57% overlap between trawling depths. The prevailing oceanographic feature for the holotype capture location is predominately a cold subantarctic Humboldt Current, whereas the Gulf of Mexico capture area is primarily influenced by the much warmer Gulf Stream. There is a high degree of invertebrate and fish species endemism for the holotype capture area (Parin *et al.* 1997); however, the paucity of research effort for the Gulf of Mexico capture area (with the exception of the marine mammal/predator prey survey, annual Gulf of Mexico surveys are limited to < 500 m bottom depth, Grace *et al.* 2010) and the noted capture site habitat differences precludes a meaningful endemic comparison between capture locations.

Conclusions. Comparisons between the holotype and the Gulf of Mexico *Mollisquama* specimen are complicated by the possibility of undocumented sexual dimorphism and ontogenic allometry, as the two known specimens are the juvenile male Gulf of Mexico specimen and the much larger female holotype of *M. parini*. Another factor to consider is that the spiral valve and liver were described for the holotype of *M. parini* but were not inspected for the Gulf of Mexico specimen; considering the rarity of *Mollisquama* and the number of features in need of proper attention a minimally invasive form of internal inspection (i.e. radiograph) was utilized until additional studies can be completed. For the purposes of documenting the capture of the Gulf of Mexico specimen, our designation as *Mollisquama* sp. is provisional since confirmation based on similarities with the description of *M. parini* was inconclusive, and several of the Gulf of Mexico *Mollisquama* features were not noted for the holotype.

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References

Claes, J.M., Nilsson, D.-E., Straube, N., Collin, S.P. & Mallefet, J. (2014) Iso-luminance counterillumination drove bioluminescent shark radiation. *Scientific Reports*, 4, 1–7. Available from: http://www.nature.com/srep/2014/140310/srep04328/full/srep04328.html (Acessed 16 Apr. 2015)

Compagno, L.J.V. (1984) *FAO Species Catalog. Vol. 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date*. FAO, Rome, 249 pp. Available from: http://www.fao.org/docrep/009/ad123e/ad123e00.htm (Acessed 16 Apr. 2015)

Compagno, L., Dando, M. & Fowler, S. (2005) *Sharks of the World*. Princeton University Press, Princeton, NJ, 368 pp.

Dolganov, V.N. (1984) A new shark from the family Squalidae caught on the Naska Submarine Ridge. *Zoologicheskii zhurnal*, 63, 1589–1591. [in Russian]

Ebert, D.A., Fowler, S. & Compagno, L. (2013) *Sharks of the World: A fully illustrated guide*. Wild Nature Press, Plymouth, NH, 528 pp.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
http://dx.doi.org/10.1111/j.1095-8649.2002.tb01723.x

Gadig, O.B.F. & Gomes, U.L. (2002). First report on embryos of *Isistius brasiliensis*. *Journal of Fish Biology*, 60, 1322–1325.
http://dx.doi.org/10.1111/j.1095-8649.2002.tb01723.x

Garrick, J.A.F. (1960) Studies on New Zealand Elasmobranchii. Part XII. The species of *Squalus* from New Zealand and Australia; and a general account and key to the New Zealand Squaloidea. *Transactions of the Royal Society of New Zealand*, 88, 519–557. Available from: http://rsnz.natlib.govt.nz/volume/rsnz_88/rsnz_88_03_005790.html (Acessed 16 Apr. 2015)

Garrick, J.A.F. & Springer, S. (1964) *Isistius plutodus*, a new squaloid shark from the Gulf of Mexico. *Copeia*, 1964, 678–682.
http://dx.doi.org/10.2307/1441443

Grace, M.A., Noble, B., Ingram, W., Pollack, A. & Hamilton, A. (2010) Fishery-independent Bottom Trawl Surveys for Deep-water Fishes and Invertebrates of the U.S. Gulf of Mexico, 2002–08. *Marine Fisheries Review*, 72, 20–25. Available from: http://spo.nmfs.noaa.gov/mfr724/mfr7242.pdf (Acessed 16 Apr. 2015)

Hertwig, O. (1874) Ueber den Bau der Placoidschuppen und der Zähne der Selachier. *Jenaische Zeitschrift fuer Naturwissenschaft*, 8, 331–404. [in German]. Available from: http://www.biodiversitylibrary.org/item/35290#page/341/mode/1up (Acessed 16 Apr. 2015)

Hulley, P.A. & Penrith, M.J. (1966) *Euprotomicroides zantedeschia*, a new genus and species of pigmy dalatiid shark from South Africa. *Bulletin of Marine Science*, 16, 222–229. Available from: http://www.ingentaconnect.com/content/umrsmas/bullmar/1966/00000016/00000002/art00004 (Acessed 16 Apr. 2015)

Hubbs, C.L., Iwai, T. & Matsubara, K. (1967) External and internal characters, horizontal and vertical distribution, luminescence, and food of the dwarf pelagic shark, *Euprotomicrus bispinatus*. *Bulletin of the Scripps Institution of Oceanography*, 10, 1–81. Available from: http://escholarship.org/uc/item/0868j08s (Acessed 16 Apr. 2015)

Klimley, P.A. (2013) *The biology of sharks and rays.* The University of Chicago Press, Chicago & London, 163. Available from: http://onlinelibrary.wiley.com/doi/10.1111/jfb.12373/abstract (Acessed 16 Apr. 2015)

Munk, O. & Jørgensen, J.M. (1988) Putatively luminous tissue in the abdominal pouch of a male dalatiine shark, *Euprotomicroides zantedeschia* Hulley & Penrith, 1966. *Acta Zoologica*, 69, 247–251.
http://dx.doi.org/10.1111/j.1463-6395.1988.tb00921.x

Naylor, G.J.P., Ryburn, J.A., Fedrigo, O. & López, A. (2005) Phylogenetic relationships among the major lineages of modern

elasmobranchs. *In:* Hamlett, W.C., Jamieson, B.G.M. (Eds.), *Reproductive Biology and Phylogeny of Chrondrichthyes: Sharks, Batoids, and Chimaeras*. Science Publishers, Inc., Enfield, NH, 3, 1–25. Available from: http://prosper.cofc.edu/~sharkevolution/pdfs/Elasmobranch_phylogeny.pdf (Acessed 16 Apr. 2015)

Naylor, G.J., Caira, J.N., Jensen, K., Rosana, K.A.M., White, W.T. & Last, P.R. (2012) A DNA sequence-based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. *Bulletin of the American Museum of Natural History*, 367, 1–262.
http://dx.doi.org/10.1206/754.1

Parin, N.V., Mironov, A.N. & Nesis, K.N. (1997) Biology of the Nazca and Sala y Gòmez Submarine Ridges, an outpost of the Indo-West Pacific fauna in the eastern Pacific Ocean: Composition and distribution of the fauna, its communities and history. *In:* Blaxter, J.H.S., Southward, A.J., Gebruk, A.V., Southward, E.C. & Tyler, P.A. (Eds.), *Advances in Marine Biology.* Academic Press, San Diego, CA, 145–242. Available from: http://www.sciencedirect.com/science/article/pii/S0065288108600176 (Acessed 16 Apr. 2015)

Peach, M.B. (2003) Inter- and intraspecific variation in the distribution and number of pit organs (free neuromasts) of sharks and rays. *Journal of Morphology*, 256, 89–102.
http://dx.doi.org/10.1002/jmor.10078

Peach, M.B. & Marshall, N.J. (2009) The comparative morphology of pit organs in elasmobranchs. *Journal of Morphology*, 270, 688–701.
http://dx.doi.org/10.1002/jmor.10715

Raschi, W. & Tabit, C. (1992) Functional aspects of placoid scales: a review and update. *Australian Journal of Marine and Freshwater Research*, 43, 123–147.
http://dx.doi.org/10.1071/MF9920123

Reif, W.-E. (1985) Functions of scales and photophores in mesopelagic luminescent sharks. *Acta Zoologica*, 66, 111–118.
http://dx.doi.org/10.1111/j.1463-6395.1985.tb00829.x

Seigel, J.A. (1978) Revision of the dalatiid shark genus *Squaliolus*: anatomy, systematics, ecology. *Copeia*, 1978, 602–614.
http://dx.doi.org/10.2307/1443686

Shirai, S. & Nakaya, K. (1992) Functional morphology of feeding apparatus of the cookie-cutter shark, *Isistius brasiliensis* (Elasmobranchii, Dalatiinae). *Zoological Science*, 9, 811–821. Available from: http://cat.inist.fr?aModele=afficheN&cpsidt=4440329 (Acessed 16 Apr. 2015)

Springer, V.G. & Garrick, J.A.F. (1964) A survey of vertebral numbers in sharks. *Proceedings of the United States National Museum*, 116, 73–96.
http://dx.doi.org/10.5479/si.00963801.116-3496.73

Stehmann, M. & Krefft, G. (1988) Results of the research cruises of FRV "Walter Herwig" to South America. LXVIII. Complementary redescription of the dalatiine shark *Euprotomicroides zantedeschia* Hulley & Penrith, 1966 (Chondrichthyes, Squalidae), based on a second specimen from the western south Atlantic. *Archiv fur Fischereiwissenschaft*, 30, 1–30.

Strasburg, D.W. (1963) The diet and dentition of *Isistius brasiliensis*, with remarks on tooth replacement in other sharks. *Copeia*, 1963, 33–40.
http://dx.doi.org/10.2307/1441272